

ORIGINAL ARTICLE

Crustacean parasites associated with hermit crabs from the western Mediterranean Sea, with first documentation of egg predation by the burrowing barnacle *Trypetesa lampas* (Cirripedia: Acrothoracica: Trypetesidae)

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Abstract

Parasitic isopods (family Bopyridae) and burrowing barnacles (family Trypetesidae) infesting hermit crabs were investigated from shallow subtidal collections made along the southeastern coast of Spain in 2009. A total of 713 specimens of *Clibanarius erythropus* (Latreille, 1818) and 82 *Calcinus tubularis* (L., 1767) were examined. Gastropod shells and worm tubes inhabited by hermit crabs were collected by hand while snorkeling and were cracked to determine host species, size, sex and presence of eggs. Two species of bopyrid isopods were found on *C. erythropus*: the branchial parasite *Bopyrissa fraiseii* (Carayon, 1943) and the abdominal parasite *Parathelges cardonae* Codreanu and Codreanu in Codreanu, 1968. Among all *C. erythropus* examined, *Bopyrissa fraiseii* was found on 0.6% of hermit crabs and *P. cardonae* was found on 0.3%. A redescription of *P. cardonae* is provided and the species is documented with light and scanning electron microscopy for the first time. No *Calcinus tubularis* harbored parasitic isopods, but one specimen was parasitized by an unidentified rhizocephalan barnacle of the genus *Septosaccus* (1.2%). The burrowing barnacle *Trypetesa lampas* (Hancock, 1849) was found associated with both hermit crab species and evidence of predation on host eggs by this barnacle is shown for the first time. *Trypetesa lampas* was found in 4.2% of the shells collected. The present study expands our knowledge of the parasite fauna of hermit crabs from the Mediterranean Sea and indicates that additional research is needed to determine the impact of trypetesid egg predators on hermit crab populations.

Key words: Bopyridae, egg predator, Isopoda, parasitism, Rhizocephala.

INTRODUCTION

Hermit crabs from shallow subtidal regions of the Mediterranean have been studied in detail in terms of their ecol-

ogy and shell use patterns. In particular, *Clibanarius erythropus* (Latreille, 1818) and *Calcinus tubularis* (L., 1767) have been intensively studied (e.g. Botelho & Costa 2000; Pessani *et al.* 2000; Benvenuto & Gherardi 2001; Gherardi & Benvenuto 2001; Benvenuto *et al.* 2003; Gherardi 2004; Caruso & Chemello 2009; Tricarico *et al.* 2009). Like most hermit crabs, these species occupy empty gastropod shells for shelter, although female *C. tubularis* are also known to occupy tubes of polychaete worms (Gherardi 2004). *C. erythropus* use various methods to

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obtain shells, including attending sites of gastropod predation (Tricarico *et al.* 2009). They are able to detect the odors released when snails are digested and can follow this trail to areas of predation. Crabs wearing lighter or damaged shells are more likely to aggregate than larger crabs that inhabit larger, heavier shells (Caruso & Chemello 2009). Shell use by *C. erythropus* has been studied both in the Mediterranean and from specimens collected along the Atlantic coast of Europe (Benvenuto & Gherardi 2001).

In spite of the extensive studies on the biology and ecology of these hermit crabs, few studies have been completed on their symbionts (Altès 1962; Basile *et al.* 2004; Williams & McDermott 2004; Bick 2006; Tirelli *et al.* 2006). In addition to the aforementioned shell attributes that are well-studied, shell associates (e.g. epibionts and endolithic species) might also influence shell choice by hermit crabs (Williams & McDermott 2004). Hermit crabs are known to act as hosts for a wide range of symbionts, including commensal species that live on or in the shells they occupy, as well as endo and ectoparasites of the crabs (McDermott *et al.* 2010). The present study reports on parasitic isopods, rhizocephalans and the burrowing barnacle *Trypetesa lampas* associated with *C. erythropus* and *C. tubularis* from the southeastern coast of Spain.

Hermit crabs are hosts to ectoparasitic isopods of the family Bopyridae, including branchial parasitic isopods (subfamily Pseudioninae) and abdominal parasitic isopods (subfamily Athelginae). In the Mediterranean, only 6 species of isopod parasites have been found associated with hermit crabs: the athelgine isopods *Asymmetrione foresti* (Bourdon, 1968) on *Paguristes eremita* (L., 1767); *Athelges tenuicaudis* Sars, 1898 on *Anapagurus breviaculeatus* Fenizia, 1937, *Parathelges cardonae* Codreanu and Codreanu in Codreanu, 1968 on *C. erythropus*; *Parathelges carolii* Codreanu, 1968 on *Dardanus arrosor* (Herbst, 1796); *Parathelges racovitzae* Codreanu, 1940 on *Diogenes pugilator* (Roux, 1828); and the pseudionine isopod *Bopyrissa fraiseii* (Carayon, 1943) on *C. erythropus*. Hermit crabs also act as hosts for rhizocephalan barnacles (Cirripedia: Rhizocephala) and 5 species have been found associated with these hosts from the Mediterranean (Øksnebjerg 2000; McDermott *et al.* 2010).

In addition to the above strict parasites, hermit crabs are hosts to burrowing barnacles of the family Trypetesidae. The 2 genera (*Tomlinsonia* and *Trypetesa*) within this family are composed of species that exclusively inhabit gastropod shells occupied by hermit crabs (Spivey 1979; Williams & McDermott 2004). In total, 2 extant species of *Tomlinsonia* are known: *T. asymetrica* (Turquier & Carton, 1976) and *T.*

mclaughlinae Williams and Boyko, 2006. There are 5 known extant species of *Trypetesa*: *T. habei* Utinomi, 1962, *T. lampas* (Hancock 1849), *T. lateralis* Tomlinson, 1953, *T. nassarioides* Turquier, 1967 and *T. spinulosa* Turquier, 1976. The type species of the latter genus, *T. lampas*, is by far the best-studied trypetesid, with many studies completed on its biology, ecology and reproduction (see reviews in Baluk & Radwanski 1991; Williams & McDermott 2004). However, the diet of *T. lampas* remains incompletely understood.

The objectives of this research were to investigate the morphology and prevalence of parasitic isopods and barnacles associated with *C. erythropus* and *C. tubularis* collected from the western Mediterranean Sea in Spain. Light and scanning electron microscopy were used to examine the taxonomically important features of these parasites. Egg predation by *T. lampas* on hermit crab hosts is described for the first time and this behavior is discussed with reference to their currently accepted status as obligate commensals.

MATERIALS AND METHODS

Hermit crabs (*C. erythropus* and *C. tubularis*) were collected in shallow subtidal areas by hand while snorkeling from July through August, 2009 along the southeastern coast of Spain (collector: J. Williams). From these collections, some hermit crabs were examined alive and the remaining crabs were fixed in 70% ethanol. The species of shell and crab were identified and measured. The shell length, aperture width and anterior shield length (SL) of hermit crabs were recorded. Each crab was removed from its shell and searched for parasitic isopods and rhizocephalan barnacles. Shells were then examined for the boring barnacle *T. lampas* after cracking with bone cutters or a metal mortar and pestle. Additional symbionts including copepods and polychaete worms that were found in the shells were noted and set aside for future studies. An ocular micrometer was used to measure isopods and eggs. The total length of isopods is reported from the anterior margin of the head or the oostegites to the posterior margin of the pleopods or the uropods. The long axis of eggs was measured for hermit crab hosts and *T. lampas*.

Line drawings of the symbionts were made with a drawing tube attachment; original sketches were scanned and traced using Adobe Illustrator. Preserved specimens were prepared for scanning electron microscopy by dehydrating in an ascending ethanol series (70–100% EtOH), ending with 4 changes of 100% EtOH. A Samdri 795 Critical Point Dryer (Tousimis; Rockville, MD) was used to dry specimens that were then mounted on aluminum stubs,

coated with gold using an EMS-550 Sputter coater (Electron Microscope Sciences; Hatfield, PA), and viewed with a Hitachi S-2460N scanning electron microscope (SEM) (Hitachi; Pleasanton, CA).

Voucher specimens were deposited in the National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM).

RESULTS

In total, 795 hermit crabs were examined: 713 specimens of *C. erythropus* and 82 specimens of *C. tubularis*. One rhizocephalan was found associated with *C. tubularis* (prevalence = 1.2%; 1 of 82), provisionally identified as a member of the genus *Septosaccus* (Fig. 1a); no *C. erythropus* were parasitized by rhizocephalans. This is the first report of a parasite on *C. tubularis* (McDermott *et al.* 2010), but further analysis of this rhizocephalan awaits collection of additional specimens. Two species of bopyrids were found parasitizing *C. erythropus* (neither was associated with *C. tubularis*): the branchial parasite *B. fraiseii* and the abdominal parasite *P. cardonae*. Finally, the burrowing barnacle *Trypetesa lampas* was found associated with both hermit crab species. The bopyrids and *T. lampas* are treated in detail below.

Systematics

Family Bopyridae Rafinesque-Schmaltz, 1815

Subfamily Pseudioninae Codreanu, 1967

Genus *Bopyrissa* Nierstrasz and Brender á Brandis, 1931

Bopyrissa fraiseii (Carayon 1943)

Figs 1b and 2

Pseudione fraisei Kossmann in Rodríguez Femenías, 1887 (*nomen nudum*).

Pleurocrypta balearica Giard and Bonnier, 1887 (*nomen nudum fide* Bourdon, 1968).

Palaegyge fraisei Giard and Bonnier, 1890 (*nomen nudum fide* Bourdon, 1968).

Pseudione fraisei Bonnier, 1900 (*nomen nudum fide* Bourdon, 1968).

Pseudione fraisei Carayon, 1943: 43–46, Figs 1–5.

Urocryptella fraisei Codreanu and Codreanu, 1963: 285.

Bopyrissa fraiseii Bourdon, 1968: 314–319, Figs 134–138; Markham, 2003: 72; Junoy and Castelló, 2003: 302; McDermott *et al.* 2010, table 1.

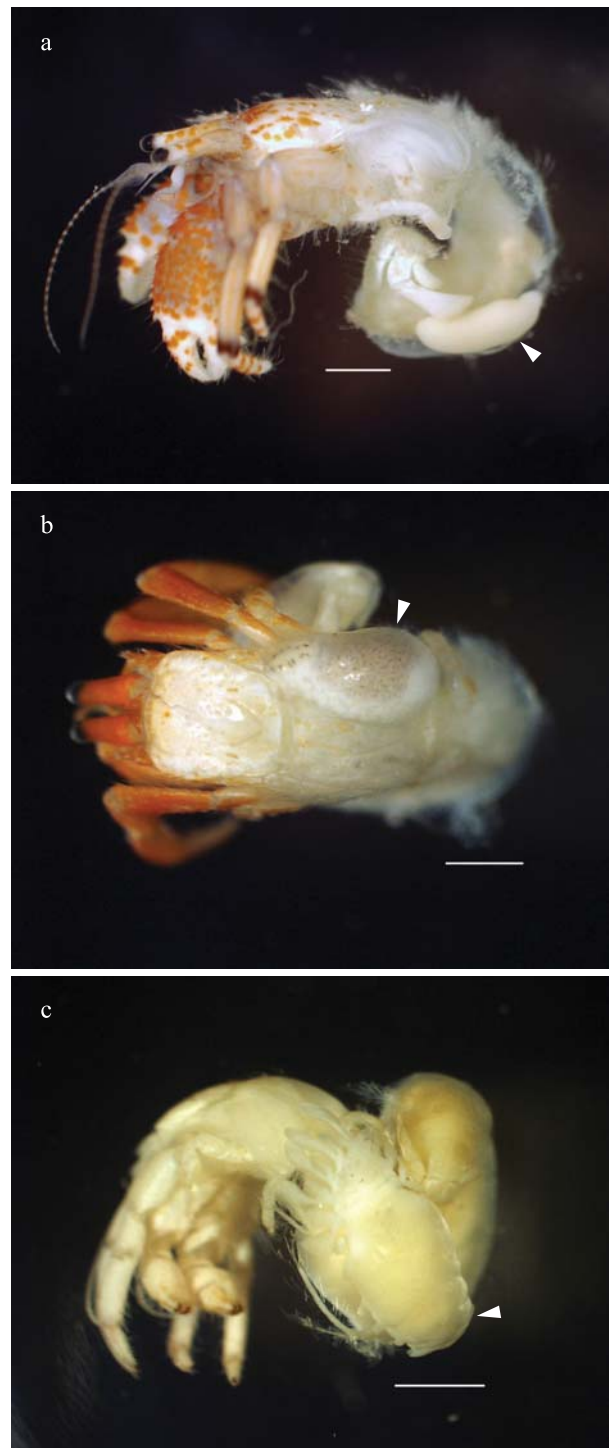


Figure 1 Arthropod parasites of Mediterranean hermit crabs. (a) The rhizocephalan barnacle *Septosaccus* sp. on *Calcinus tubularis*; (b) The pseudionine isopod *Bopyrissa fraiseii* on *Clibanarius erythropus*; and (c) The athelgine isopod *Parathelges cardonae* on *Clibanarius erythropus*. Arrowheads show position of parasites on hosts. The scale bars: a–c = 1 mm.

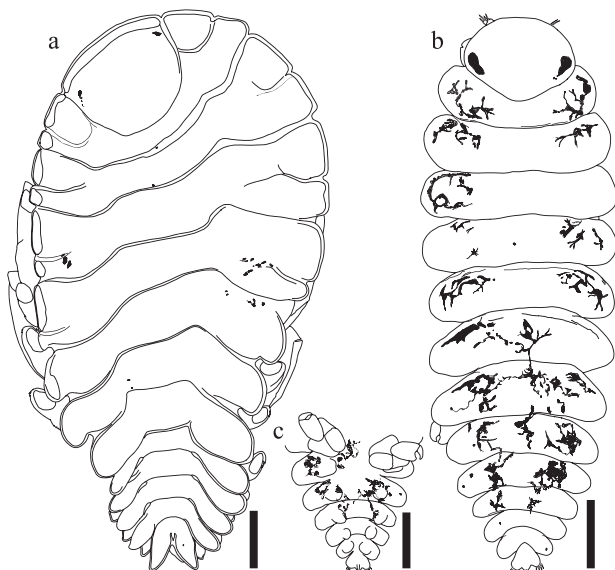


Figure 2 The pseudonine isopod *Bopyrissa fraiseii*: female (a), male (b) and (c). (a) Female, dorsal view; (b) male, dorsal view; and (c) pleon, ventral view. The scale bars: a = 200 µm; b, c = 100 µm.

Material examined: Dextral ovigerous female (2.5 mm) and male (0.8 mm) in right branchial chamber of female *C. erythropus* (2.1 mm SL) occupying shell of *Cerithium* sp., Spain, Cartagena, Cabo de Palos (37°26'2.13"N, 1°28'59.22"W), shallow subtidal, collected by J. D. Williams, 6 August 2009 (USNM 1147913); dextral juvenile female (1.3 mm) in right branchial chamber of male *C. erythropus* (1.2 mm SL) occupying shell of *Cerithium* sp., Spain, Cartagena, Playa de Cala Reona (37°37'1.25"N, 0°42'53.70"W), shallow subtidal, collected by J. D. Williams, 6 August 2009 (USNM 1147914); dextral ovigerous female (2.0 mm) and male (0.8 mm) in right branchial chamber of female *C. erythropus* (1.8 mm SL) occupying shell of *Cerithium* sp., Spain, Cartagena, Cabo de Palos (37°37'54.97"N, 0°41'27.38"W), shallow subtidal, collected by J. D. Williams, 16 August 2009 (USNM 1147915); dextral ovigerous female (2.1 mm) and male (0.9 mm) in right branchial chamber of male *C. erythropus* (2.0 mm SL) occupying shell of *Cerithium* sp., Spain, Cartagena, Cabo de Palos (37°37'54.97"N, 0°41'27.38"W), shallow subtidal, collected by J. D. Williams, 16 August 2009 (USNM 1147916).

Remarks: This species was redescribed in detail by Bourdon (1968) based on specimens parasitizing *C. erythropus* collected in France; the new specimens from

Spain (Figs 1b and 2) closely match his description. The adult females from Spain were all slightly dextral, occupying the right branchial chamber of hosts and possessing small eyespots. Of the females, 3 were ovigerous, the largest specimen reaching 2.5 mm in length. The males have large eyes and scattered pigmentation on the pereon and pleon (Fig. 2b). The males possess rounded pleopods on pleomeres 1–5 and stout terminal setae on the final pleomere, lateral to the anal cone (Fig. 2c). The largest male was 0.9 mm in length.

Ecology: 0.6% (4 of 713) of *Clibanarius erythropus* were infested by *Bopyrissa fraiseii*; all specimens were found in the right branchial chamber of hosts.

Distribution and hosts: Mediterranean coasts of France and Spain, Balears Islands and Corsica on *C. erythropus*; Atlantic coast of France (Bassin d'Arcachon, Guethary) on *C. erythropus*.

Subfamily Athelginae Codreanu and Codreanu, 1956
Genus *Parathelges* Bonnier, 1900

Parathelges cardonae Codreanu and Codreanu in Codreanu, 1968

Figs 1c, 3, 4

Athelges cardonae Kossmann in Rodríguez Femenías, 1887; Bonnier, 1900: 154, 169, 380 (list); Codreanu, 1961: 137, Fig. 1 (all *nomina nuda*).

Athelgue cardonae Stebbing, 1893, p. 410 (*nomen nudum*).

Parathelges cardonae Codreanu and Codreanu in Codreanu, 1968, p. 609; Markham, 2003: McDermott *et al.*, 2010, table 1.

Material examined: Ovigerous female (6.3 mm) and male (1.6 mm) on abdomen of female *C. erythropus* (2.8 mm SL) occupying unidentified gastropod shell, Spain, Cartagena, Playa de Cala Reona (37°37'1.25"N, 0°42'53.70"W), shallow subtidal, collected by J. D. Williams, 2 August 2009, (USNM 1147917); ovigerous female (7.0 mm) and male (2.3 mm) on abdomen of female *C. erythropus* (2.2 mm SL) occupying shell of *Cerithium* sp., Spain, Cartagena, Cabo de Palos (37°37'54.97"N, 0°41'27.38"W), shallow subtidal, collected by J. D. Williams, 6 August 2009 (USNM 1147918; includes male on SEM stub).

Description: Female (Figs 1c, 3a–e). Body length of largest female 7.0 mm, maximal width 2.7 mm, head length 0.7 mm, head width 0.7 mm, pleon length 2.3 mm. Body longer than broad; pereon slightly distorted sinistrally. Cephalon with convex lateral margins, ante-

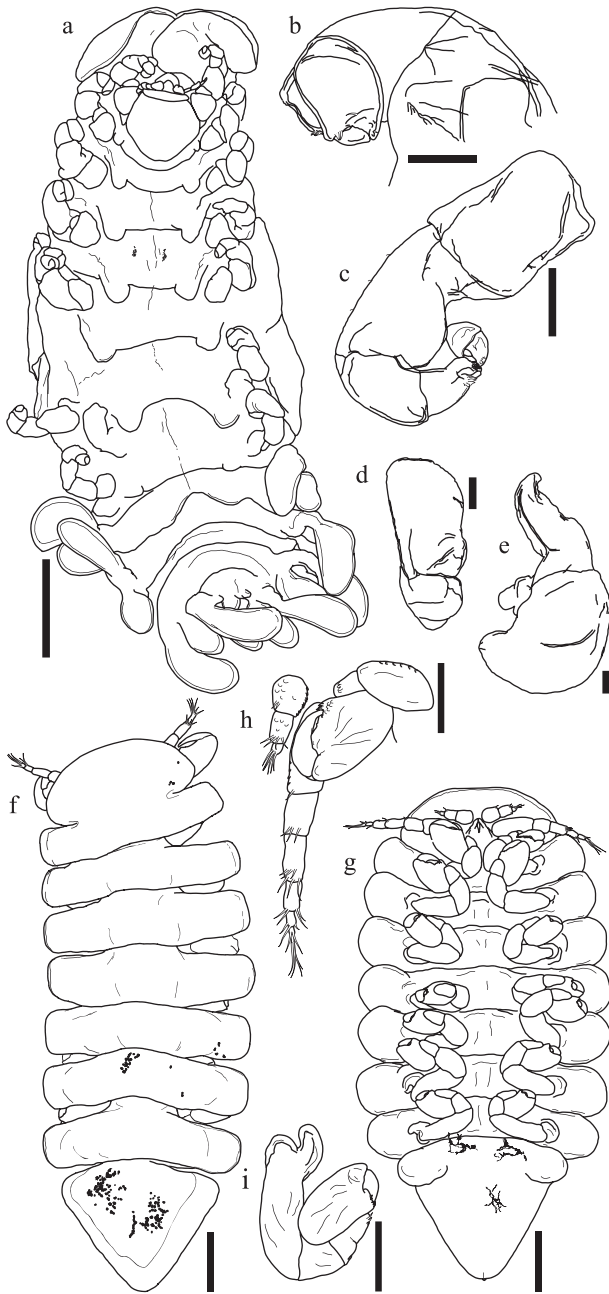


Figure 3 The athelgine isopod *Parathelges cardonae*; female (a–e), male (f–i). (a) Female, dorsal view; (b) left pereopod 1; (c) left pereopod 7; (d) left maxilliped, external view; (e) left oostegite, external view; (f) male, dorsal view; (g) male, ventral view; (h) left antennule, antenna and pereopod 1; and (i) left pereopod 7. The scale bars: a = 1 mm; b, c, h, i = 100 µm; d–f = 250 µm; g = 200 µm.

rior margin flattened, posterior margin convex. Eyes absent, slight pigmentation on pereomere 4. Cephalon overlapping median regions of pereomeres 1 and 2. Antenna of 6 articles; antennule of 3 articles, distal margins of segments with setae, most segments with scales visible. Maxilliped (Fig. 3d) with low rounded spur; palp absent.

Pereon of 7 pereomeres, broadest across pereomere 5, 6, tapering anteriorly and posteriorly. Pereomere 1 medial margin obscured by cephalon, posterior margin of pereomeres 2, 3 rounded, pereomeres 4–7 posteriorly straight to slightly convex; all posterior lateral margins with rounded lobes, largest on pereomeres 4–6 (Fig. 3a). First oostegite proximal lobe subtriangular, distal lobe with ovate distal lobe and narrow, bladelike proximal lobe, internal ridge smooth (Fig. 3e). First 2 oostegites extended over head, middle oostegites extended laterally beyond pereopods. Oostegites completely enclosing brood pouch; posterior oostegite with setae on posterior margin. Pereopod 1 smaller than 2–7, which are subequal. Pereopods 1 anterior to cephalon, 2 nearly parallel to posterior margin of cephalon, large gap between pereopods 5 and 6 (Fig. 3a).

Pleon with 6 pleomeres. Pleomeres 1–5 with rounded and pedunculate uniramous pleopods and longer, rounded, pedunculate uniramous lateral plates; pleotelson with short uniramous, digitiform uropods (uropods absent in 1 specimen due to damage).

Male (Figs 3f–i and 4). Body length 2.3 mm, maximal width 0.9 mm, head length 0.3 mm, head width 0.6 mm, pleon length 0.6 mm. Head ovate, widest posteriorly, fused with pereomere 1. Eyes absent, with slight pigment on posterolateral margin of head (Fig. 3f). Antenna (Figs 3h and 4b) of 7 articles, distally setose; extending posterolaterally from head; antennule of 3 articles, distally setose (Figs 3h and 4b).

Pereomere 4 broadest, tapering slightly anteriorly and posteriorly. Diffuse pigmentation present on pereomeres 5, 6 and pleon (Fig. 3h). All pereopods (Fig. 3g) of equal total size, all articles distinctly separated and with scales, dactylus of pereopod 1 (Figs 3h and 4b) longer than posterior pereopods (Figs 3i and 4c), dactylus with broad scales at distal end, insertion point of distal end of dactylus on propodus surrounded by stout setae, merus with numerous setae (Fig. 4c).

Pleon tapering posteriorly, all pleomeres fused but indication of segmentation ventrally on pleomere 1 in one specimen (Fig. 3g); posterior margin rounded. No midventral tubercles, pleopods, or uropods (Figs 3g and 4a).

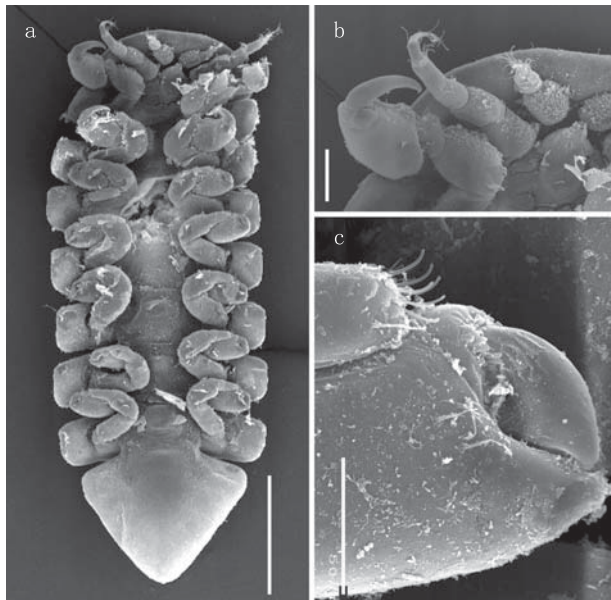


Figure 4 The athelgine isopod *Parathelges cardonae*; male, scanning electron micrographs. (a) Male, ventral view; (b) right antenna, antennule and pereopod 1; and (c) right pereopod 6, distal view. The scale bars: a, c = 500 µm; and b = 100 µm.

Remarks: *Parathelges cardonae* was erected by R. and M. Codreanu in Codreanu (1968) as a replacement for the *nomen nudum* *Athelges cardonae* Kossman in Rodríguez Femenías, 1887 (and others, see preceding synonymy list) based on specimens parasitizing *C. erythropus* from Corsica. Unfortunately, these authors only provided a short description and no figures. The females and males are herein documented for the first time with light and scanning electron microscopy. The new specimens largely match the textual description provided in Codreanu (1968).

As previously noted by Codreanu (1968), *P. cardonae* is very similar to *P. racovitzae* reported in the Black Sea and Mediterranean on *D. pugilator*. Based on the overlapping geographic distributions of *P. cardonae* and *P. racovitzae*, the fact that they both utilize ecologically similar shallow subtidal hosts (*C. erythropus* and *D. pugilator*, respectively) and their very similar morphologies, their status as distinct species should be examined. Unfortunately, the type material for *P. racovitzae* is suspected to be lost (Boyko, personal communication) so this will require new collections of parasitized *D. pugilator* from the Mediterranean and the Black Sea.

Ecology: 0.3% (2 of 713) of *C. erythropus* were infested by *P. cardonae*. Bourdon (1968) reported preva-

lence of 0.5–2% for this species on the same host in other areas of the Mediterranean.

Distribution and hosts: Mediterranean coasts of Africa, Spain, Balears Islands and Corsica, on *C. erythropus*.

Infraclass Cirripedia Burmeister, 1834

Superorder Acrothoracica Gruvel, 1905

Family Trypetesidae Stebbing, 1910

Genus *Trypetesa* Norman, 1903

Trypetesa lampas (Hancock, 1849)

Figs 5 and 6

Alcippes lampas Hancock, 1849: 313–14, pls. 8–9; Darwin, 1854: 530–63, pl. 22, figs 1–15, pl. 33, figs 16–19; Hoek, 1876, 55; Hoek, 1883: 3, 29; Weltner, 1897a: 446; Weltner, 1897b: 238; Aurivillius, 1894: 72, 75–8, 81, 82, pl. 6, figs 1 and 5–9, pl. 7, figs 7–21, pl. 9, figs 4 and 9; Berndt, 1903: 396–457, pls. 19–22; Gruvel, 1905: 323–8, figs 336–9; Norman, 1903: 369; Genthe, 1905: 181–200, pls. 11–12; Nilsson-Cantell, 1921: 78–92, 123–6 and 129, figs 13 and 21; Kühnert, 1934: 45–78, figs 1–24; Jensen and Bender, 1973: 190, table 1 and fig. 3; Cuadras and Pereira, 1977: 304.

not Wells, 1961: 248 (= *Kochlorine floridana* Wells and Tomlinson, 1966).

Alcippes lampas gigantea Berndt, 1907: 289.

Trypetesa lampas Tomlinson, 1953: 373, fig. 1; Tomlinson, 1955: 97, 100–102, 106, 111; Utinomi, 1964: 118, 125, 128; Zullo, 1964: 89, 91; Hagerman, 1965; Boekschoten, 1966: 370–74, figs 12, 13, 15 and 16; Kauri, 1966: 120; Turquier, 1967: 33–35, 40, 43, 46, fig. 8; Seilacher, 1969: 709, 715, figs 1 and 6, pl. IV; Tomlinson, 1969: 7, 11, 14–15, 17, 19–20, 22, 24–6, 28, 126, 131–2, 147, 150, 153, fig. 36, table 2; White, 1969: 333–9, figs 3–5; Turquier, 1970: 572, 574, 576, 577, 590, 611, 612, 614, 620, fig. 3; White, 1970: 29, 33, fig. 2; Weisbord, 1975: 179–81, pl. 20, figs 4 and 5; Spivey, 1979: 498–502, figs 1–3; Zullo, 1979: 1, 24; Kamens, 1981: 103 pp.; Rittschof *et al.*, 1983: 495, 496, 499, 500; Grygier and Newman, 1985: 17–19, fig. 8; Lambers and Boekschoten, 1986: 257, 258, 261, 264, fig. 1; Klepal, 1987: 251, 259–260, 294, 297; Tomlinson, 1987: 67, fig. 4; Turquier, 1987: 401–7, figs 9–13; Barnes, 1989: 73–8; Baluk and Radwanski 1991: 13, 21, 23–31, figs 7 and 8; Gotelli and Spivey, 1992: 474–9, figs 1–5; Walker, 1992: 547; Anderson, 1994: 162, 178; Jensen *et al.*, 1994: 127, 129, fig. 3, table 1; Moyse *et al.*, 1995: 157, 161, 168, 169, 171, 173, pl. 1, tables 1, 2; Høeg *et al.*, 1998: 195–7, 200,

203, figs 1–3, 5 and 6; Kolbasov 1999: 142; McDermott, 2001: 626, 628 (list); Kolbasov, 2002: 85, 92, 93, fig. 5G–K; McGrath and Holmes, 2003: 234–5; Reiss *et al.*, 2003: 409, 412, 413, tables 3 and 5; Williams and McDermott, 2004: 34 (list), 73–75; Williams and Boyko, 2006: 294; Newman, 2007: 476, 481, pl. 214; Kolbasov and Høeg, 2007: 129–30, figs 3, 5 and 11; Murphy, 2008: 8, 10–12, 15, 16, 19–25, 33, 42, 43, 54, 56, 58, 60–62, 64; Deutsch, 2009: 319, fig. 3; Deutsch, 2010: 104, 105, fig. 5.

not Rosell, 1976: 278, 302, 305, pl. XII (= sp. indet. *vide* Williams & Boyko, 2006).

Material examined: 2 barnacles from unidentified gastropod shells occupied by *C. erythropus*, Spain, Aguilas, Ensenda de la Fuente (37°26'2.13"N, 1°28'59.22"W), shallow subtidal, collected by J. D. Williams, 29 July 2009 (personal collection); 8 barnacles from shells of *Cerithium* sp., *Columbella* sp. and *Stramonita* sp. occupied by *C. erythropus* and *C. tubularis*, Spain, Cartagena, Playa de Cala Reona (37°37'1.25"N, 0°42'53.70"W), shallow subtidal, collected by J. D. Williams, 2 August 2009 (USNM 1147919); 10 barnacles from shells of *Cerithium* sp., *Columbella* sp. and *Nitidella*-like sp. occupied by *C. erythropus* and *C. tubularis*, Spain, Cartagena, Playa de Cala Reona (37°37'1.25"N, 0°42'53.70"W), shallow subtidal, collected by J. D. Williams, 5 August 2009 (USNM 1147920); 10 barnacles from shells of *Cerithium* sp., *Comus* sp., *Fasciolaria* sp., *Osilinus* sp., *Nitidella*-like sp. and *Stramonita* sp. occupied by *C. erythropus* and *C. tubularis*, Spain, Cartagena,

Cabo de Palos (37°37'54.97"N, 0°41'27.38"W), shallow subtidal, collected by J. D. Williams, 6 August 2009 (USNM 1147921); 3 barnacles from shells of *Cerithium* sp., *Osilinus* sp. and *Nitidella*-like sp. occupied by *C. erythropus*, Spain, Cartagena, Cabo de Palos (37°37'54.97"N, 0°41'27.38"W), shallow subtidal, collected by J. D. Williams, 16 August 2009 (personal collection).

Description: Female 5.4 mm maximal length, 2.3 mm maximal width (Fig. 5a). Mantle laterally compressed, muscular, oriented ventrally to aperture, body bluntly rounded at distal end or extending to broader lobes conforming to spiral of shell (Fig. 5a). Aperture slit-like opening on columella of shell typically with curved tapered end. Opercular bars symmetrical, posterior (rostral) end thin with low rounded orificial palps, with shallow depression toward thickened and flattened carinal (anterior) margin (Fig. 6a). Attachment process (horny knob) posterior to rostral end, attachment disk dorsal to the ovaries. Outer surfaces of opercular bars with horizontal rows of denticles and setae (Fig. 6a and b); inner surface with rows of setae and unifid to multifid denticles (Fig. 6e and f). Four pairs of cirri. Cirrus I (mouth cirrus) biramous; protopod elongate and tubular, naked. Three pairs of terminal cirri uniramous with 4 segments (Fig. 6c); second segment with protuberant “cushion” (Fig. 6c and d) on distal inner surface of pairs 4, 5 (cushion absent on pair 6), cushion with numerous regular rows of bladelike denticles (Fig. 6d); fourth segment narrower than third,

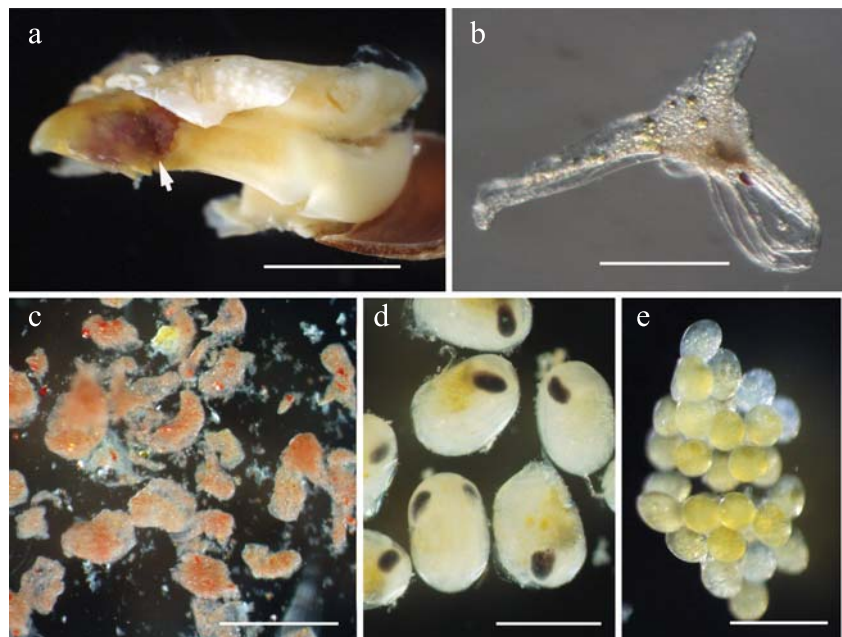


Figure 5 The burrowing barnacle *Trypetes lampas*. (a) Overview of female *T. lampas* in shell cracked to expose body of barnacle, with distended gut containing eggs of *Clibanarius erythropus* (arrow); (b) male *T. lampas*; (c) eggs of *C. erythropus* from gut of *T. lampas*; (d) preserved eggs of *C. erythropus*; and (e) eggs of *T. lampas*. The scale bars: a = 2.0 mm; b = 250 µm; c, d = 200 µm; e = 300 µm.

tapering distally, terminating in pair of bifid hooks.

Male: Minute males (approximately 500 µm in length) found in embedment pouch on disk of female; often multiple males (up to 7) per female (Fig. 5b). Body bilobed with large lateral lobe containing sperm, lipid globules and eyespot; short digitiform lobe opposite penis. Annulated penis contained in sheath, longer than lateral lobe.

Distribution and hosts: Mediterranean coast of Spain, in shells occupied by *C. erythropus* and *C. tubularis* (new host and locality records); Mediterranean in shells occupied by *D. arrosor* (Herbst, 1796) (Cuadras & Pereira 1977); Irish Sea, North Sea and Swedish waters in shells occupied by *Pagurus bernhardus* (Linnaeus, 1758) and *P. cuanensis* Bell, 1845 (e.g. White 1969; Jensen & Bender 1973; Reiss *et al.* 2003); east coast of the USA in shells occupied by *Pagurus longicarpus* Say, 1817 and *Pagurus*

pollicaris Say, 1817 (McDermott 2001; Williams & McDermott 2004); Gulf of Mexico, Florida in shells occupied by *Pagurus impressus* (Benedict, 1892) (Spivey 1979).

Remarks: This is the first time *T. lampas* has been found with *C. erythropus* and *C. tubularis*. *T. lampas* has been described in detail multiple times from various locations around the world, including a redescription by Spivey (1979) that utilized SEM to examine the ultrastructure of specimens from the Gulf of Mexico. The present specimens from the Mediterranean are similar to previous descriptions, including SEM details of taxonomically important features. Although *T. lampas* is the best-studied trypetesid barnacle in terms of biology and ecology, some taxonomic confusion exists in this species. For example, the description of *T. lampas* from deeper water (approximately 200 m) in the Philippines by Rosell (1976) does not represent this species

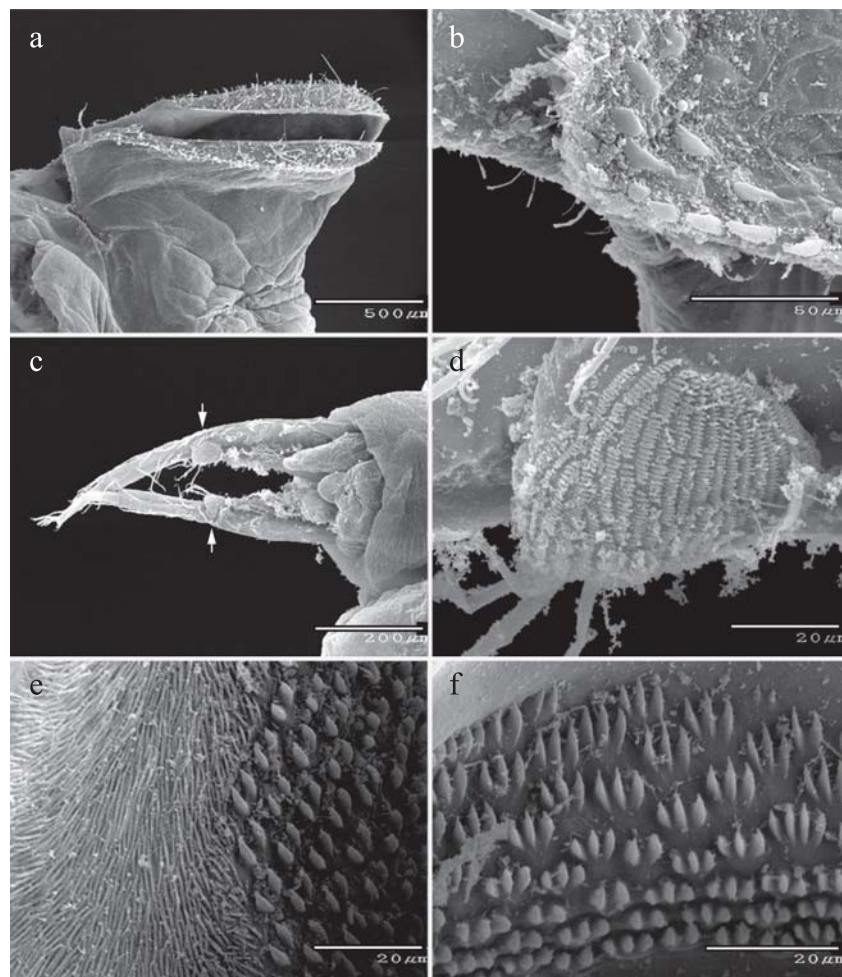


Figure 6 The burrowing barnacle *Trypetesa lampas*, scanning electron micrographs. (a) Opercular bars, oblique lateral view; (b) denticles on outside of orificial palp on right opercular bar; (c) one pair of terminal cirri, showing cirral cushions (arrows); (d) cirral cushion; (e) setae and denticles from inside of opercular bars; and (f) multifid denticles from inside of opercular bars. The scale bars: a = 500 µm; b = 50 µm; c = 200 µm; d–f = 20 µm.

and further studies are needed to determine if it is a described or new species (Williams & Boyko 2006). Along the east coast of the USA, *T. lampas* has been reported multiple times but there appears to be more than one species that exists in this region. Grygier and Newman (1985) discussed an undescribed species from North Carolina reportedly discovered by Standing and Tomlinson; however, no description or work on this species has been published. Therefore, *T. lampas* might be confused with other species and could represent a species complex.

The global distribution of *T. lampas* might be the result of human mediated introduction, as suggested for other trypetesids (Murphy 2008; Williams & Murphy in preparation). Most estuarine and marine introductions (including examples of barnacles) are strongly linked with "human transport mechanisms," usually related to shipping (e.g. Carlton & Geller 1993; Carlton & Cohen 2003). Dispersal of acrothoracicans by pelagic larval stages is considered limited compared to other barnacles (Kolbasov & Høeg 2007), yet the length of time spent in the water column by larvae of *T. lampas* remains unknown. However, unlike other trypetesids that have lecithotrophic naupliar stages and non-feeding cyprids, *T. lampas* releases free-swimming naupliar larvae (Turquier 1967, 1970), which are possibly responsible for its broad distribution. Before the use of ballast water, ships used solid ballast consisting of rocks and stones from the ocean floor. Although a less likely mode of transport, it is possible that hermit crabs (or their shells containing barnacles) could have been introduced in this material or transported in materials associated with bivalve aquaculture (Carlton & Zullo 1969).

Ecology: The prevalence of *T. lampas* in the combined samples was 4.2% (33 of 795) of the shells collected (3.8% (27 of 713) associated with *C. erythropus* and 7.3% (6 of 82) associated with *C. tubularis*). Of the *T. lampas* in shells of *C. erythropus*, 23 (85%) were associated with female hermit crabs, whereas only 4 were found with males; among *C. tubularis*, 4 (67%) were found with females, whereas 2 were found with males. Both hermit crabs had female-skewed sex ratios, yet *T. lampas* was found more often than predicted with female hermit crabs (predicted equal distribution among male and female hosts ($\chi^2_1 = 7.5$, $N = 793$, $P = 0.006$)). *T. lampas* was found in gastropod shells of the genera *Cerithium*, *Columbella*, *Conus*, *Fasciolaria*, *Osilinus*, *Nitidella* and *Stramonita*. Typically, there was 1 female *T. lampas* per shell, but 3 shells (9%) had 2 females; the average total length of the shells was 15.6 ± 2.0 (n = 21). The average size of the *C. erythropus* inhabiting the shells was 2.7 ± 0.7 mm

(n = 28) and *C. tubularis* was 3.7 ± 0.9 mm (n = 5).

Feeding: *Trypetesa lampas* is an egg predator of *C. erythropus* and *C. tubularis*. Of the *T. lampas* specimens associated with ovigerous female hosts, 82% (18 of 22) showed signs of egg predation, as evidenced by hermit crab egg corions removed from the gut, the presence of yolk in the gut (the same coloration as hermit crab eggs; Fig. 5a and c) or dark pigmentation of gut contents when feeding on hermit crabs embryos at the eyed stage (Fig. 5d). *T. lampas* was found with hermit crab eggs in early through late development in their gut. During early development the eggs of *C. erythropus* were 0.27 ± 0.02 mm (n = 25). The eggs of *C. tubularis* were 0.19 ± 0.01 mm (n = 25). The eggs of *T. lampas* contained in the body of the barnacle were 0.10 ± 0.004 mm (n = 25) (Fig. 5e).

DISCUSSION

Worldwide, there are 30 species of rhizocephalans and more than 80 species of bopyrids associated with hermit crabs (An *et al.* 2010; McDermott *et al.* 2010). However, even in relatively well-studied regions, such as the Mediterranean, the natural history of many of these species is poorly known and many undescribed species remain. Rhizocephalans are monoxenous with crustaceans as their definitive hosts, whereas bopyrids parasitize crustaceans as their definitive hosts and calanoid copepods as their intermediate hosts (Boyko & Williams 2009). Both groups can have major impacts on the fitness of hermit crabs. Rhizocephalans are parasitic castrators that can modify the behavior and physiology of hosts through hormonal influence (McDermott *et al.* 2010). Bopyrids can shut down reproduction of hosts apparently through the energy burden from feeding on host hemolymph and possibly chemical secretion (McDermott *et al.* 2010). In contrast, trypetesid barnacles do not feed on the hemolymph of hosts or chemically suppress gonad development, but they do negatively impact host reproduction as egg predators.

Most acrothoracican barnacles gather food in a similar fashion as thoracicans, using a sweeping motion of the cirral net (Tomlinson 1969; Anderson 1994). Typically, the thoracic cirri are extended through the opercular bars and used to remove food particles from the water column. Use of the cirral net to feed has been observed in several species within the Lithoglyptidae and Cryptophialidae but has never been documented within the family Trypetesidae, members of which have reduced cirri reportedly too short to form a net (Tomlinson 1969). Tomlinson (1969) did not observe cirri of trypetesids to extend beyond the opercular bars, but we have seen thoracic cirri of some *Trypetesa* to extend beyond

the opercular bars, as also noted by Utinomi (1964) for *T. habei*. Kamens (1981) concluded that *T. lampas* feeds using a filter-feeding system via expansion of the mantle, causing water to be taken in. The pumping process is continuous, with short pauses in between each expansion/contraction cycle (as noted in other trypetesids; Murphy, pers. obs.). Food particles, possibly dropped by the host or free-floating in the water, are thought to be brought in with each mantle expansion, and removed from the water by the cirri. Therefore, *T. lampas* appear to be able to capture small particles from the water after they are brought in by the pumping action of the mantle.

The present research shows that *T. lampas* is also able to feed on large food particles, specifically the eggs and developing embryos of hosts. However, the mechanics by which eggs are captured and ingested by trypetesids remains unknown. The cushions on the thoracic cirri have been suspected to aid in the handling of food (Darwin 1854; Tomlinson 1969), but no direct observations have been made to determine exactly how the cirri are used in feeding or the role of the cushions in the process. The thoracic cirri might be used to grasp a host egg, possibly gripped by the cushions, and then brought to the mouth for ingestion. The cushions were initially thought by Darwin (1854) to macerate food but it is more likely that they are involved in egg capture and manipulation to mouth cirri.

Regardless of the mechanics of egg capture, these barnacles can have significant negative impacts on the reproduction of hermit crab hosts. As evidenced by the fact that hermit crab eggs early through late development were found in the gut of *T. lampas*, it is apparent that the barnacles feed on eggs soon after attachment to pleopod setae and nearly through to the time of release of hermit crab larvae. *T. lampas* might also feed on eggs lost by hermit crabs during the normal movements and cleaning of the brood by hosts. It remains unknown if *T. lampas* is able to feed on eggs during extrusion by hermit crabs prior to attachment to pleopod setae. Evidence of feeding on multiple broods was shown by one barnacle in the study; the gut of the barnacle contained black pigmentation, whereas the host hermit crab had eggs early in development. Either the barnacle had fed on a prior brood from this hermit crab or there had been a shell switch between female hermit crab hosts. Trypetesid barnacles represent 1 of 4 phyla known to feed on hermit crab eggs (Williams 2002; Williams & McDermott 2004).

The diet of trypetesids inhabiting shells with nonovigerous females and male hermit crabs needs to be

investigated. The nutritional requirements for trypetesids are unknown and it is possible that the eggs can support their survival while associated with nonovigerous females and males. Trypetesids lack an anus, a feature that could increase gut residence time and might be explained, in part, by the behavior of egg predation. Trypetesids might also ingest host feces, as has previously been proposed (Kolbasov & Høeg 2000; Williams & Boyko 2006), but no one has tested this possibility. Kamens (1981) describes blue-green algae-like particles in the gut of *T. lampas* specimens but does not clarify the sex of the hermit crabs inhabiting the shells. It is possible that trypetesids filter feed and ingest tiny particles from the water column (e.g. algae, feces and pieces of food dropped by hermit crabs) when inhabiting a shell with a male hermit crab, and engage in egg predation when in a shell with an ovigerous hermit crab. Kamens' (1981) observations of spherical particles in the gut resemble the yolk material found in the gut of the egg predators in the present study. He concludes that the diet of trypetesids consists of tiny particles (gut particles measured 1.5 µm in diameter, thought to be algae). However, the present studies show that trypetesids can ingest eggs up to 0.2 mm in diameter.

Based on the observations of gut materials, followed by the confirmation of host eggs by histology, and the close proximity of trypetesids to host eggs, it is possible that all members of Trypetesidae are transient egg predators (Murphy 2008; Williams & Murphy in preparation). Although presently categorized as an obligate commensal relationship (one partner benefits while the other is neither harmed nor helped), trypetesids might more accurately be defined as transient parasites of hermit crabs (i.e. the barnacles harm female hosts by feeding on their eggs but can live for periods with no harmful impacts on the hosts), like certain other egg predators (Williams & McDermott 2004). The finding that the barnacles are found significantly more often with female hermit crab hosts leads to the question of why the hermit crabs do not avoid or switch shells when the egg predators are present. It might be that empty shells are limited in these populations (as found in some hermit crab populations; e.g. Kellogg 1976; Scully 1979; Faria *et al.* 2007) and the costs of switching shells for female hermit crabs outweigh the loss of eggs. In addition, their activity as shell borers potentially makes their hermit crab hosts more susceptible to shell crushing predators (Williams & McDermott 2004). More accurate understanding of this symbiosis requires exploration of the many questions remaining on the biology of these barnacles and their interactions with hermit crabs.

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